

ABSCISSION OF LEAVES IN *GREYIA* HOOK. & HARV.

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ABSTRACT

Longitudinal cortical ridges on the internodes of *Greyia* Hook. & Harv. give an erroneous impression of sheathing leaves. During abscission the epidermis and cortex of the stem abscise with the leaves. The separation layer, as well as the phellogen of the protective layer, is already present in the shoot apex. The phellogen originates in the pericycle.

UITTREKSEL

AFSNOERING VAN BLARE BY *GREYIA* HOOK. & HARV.

Lengteverlopende korteksriwwe op die stingellitte van *Greyia* Hook. & Harv. skep 'n vals indruk van blaarskedes. Gedurende blaarval word die stinglepidermis en -korteks saam met die blare afgesnoer. Die skeidingslaag, sowel as die fellogeen van die beskermingslaag, is reeds in die stingelgroeipunt aanwesig. Die fellogeen ontstaan in die perisikel.

INTRODUCTION

Greyia Hook. & Harv., an endemic genus, closely related to *Bersama* Fresen and *Melianthus* Linn. (Scholz, 1964), is represented in South Africa by three species, viz. *G. sutherlandii* Hook. & Harv., *G. radlkoferi* Szyszyl and *G. flanaganii* H. Bol. The first two species are shrubby, deciduous trees, while *G. flanaganii* is an evergreen shrub.

The leaves of *Greyia* are subrotund or heart-shaped and palmately veined with cylindrical petioles. The leaf bases are dilated and partly encircle the nodes. Organographically, however, each leaf seems to continue as a long sheath lying close to the stem and extending through the entire preceding internode (fig. 1). This characteristic of *Greyia* is regarded by Hutchinson (1959) as "petioles sheathing at the base", while Phillips (1951) mentions "petioles dilated at the base".

At the end of the growing season the leaves of *G. sutherlandii* and *G. radlkoferi* abscise acropetally along the leaf bearing shoots. Abscission of a leaf does not, however, occur at the leaf base, but commences at the margins of the "sheath", near the base of the preceding internode (fig. 2). In this way, the appearance of a sheathing leaf is heightened.

Although *G. flanaganii* is not deciduous, older leaves abscise in the same way.

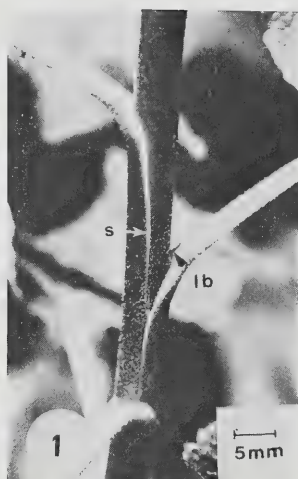


FIG. 1.

A part of the one year old shoot of *Greyia flanaganii*, illustrating the leaf base and "leaf sheath": lb, leaf base; s, "sheath".



FIG. 2.

A part of the one year old shoot of *G. sutherlandii* illustrating the abscising tissues: bi, base of internode; s, "sheath".

An anatomical study of the stems of all three species of *Greyia* was therefore undertaken to investigate the interesting and unusual abscission phenomenon found in this genus.

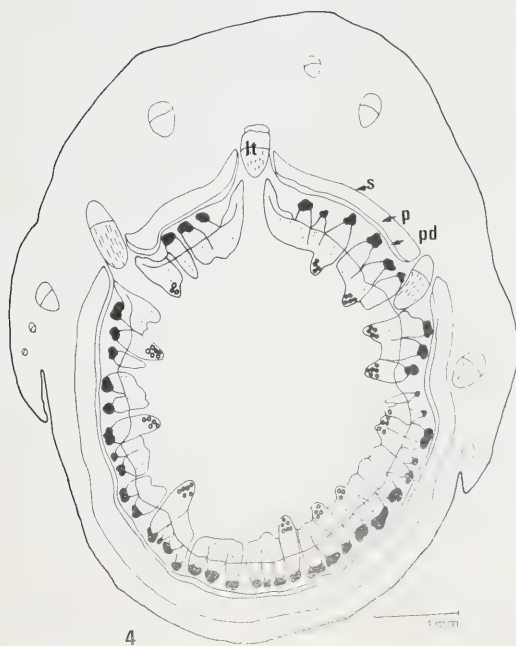
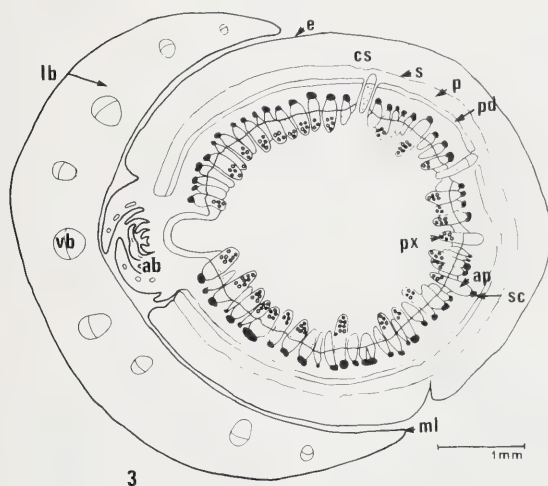
MATERIAL AND METHODS

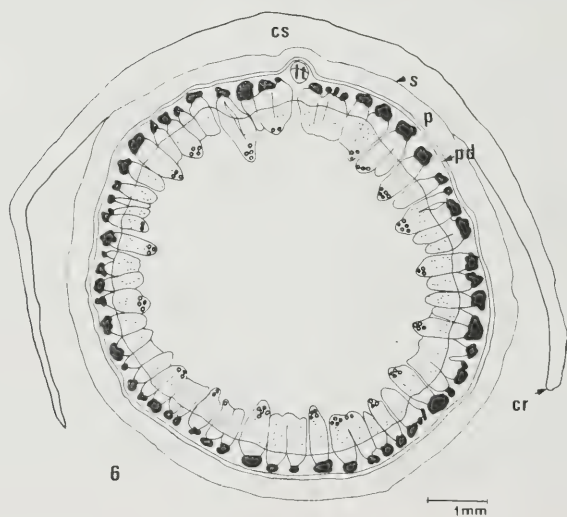
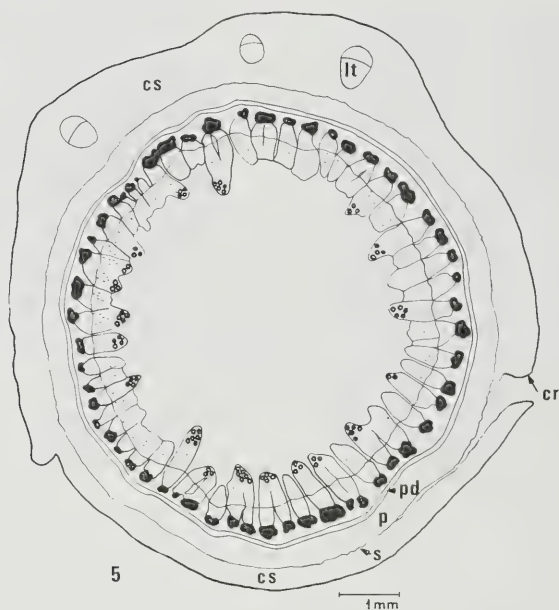
Stem apices and segments of one year old shoots of all three species of *Greyia* Hook. & Harv. were fixed during June 1973 in 6% glutaraldehyde at 0°C in a 0.025 M phosphate buffer at pH 6.8 (Feder and O'Brien, 1968) and in formalin-acetic acid-alcohol (F.A.A.). After dehydration and impregnation with either wax or a mixture of glycol methacrylate (Ashley and Feder, 1966), transverse sections were cut.

Wax sections were stained with safranin and "Fast Green FCF" (Gürr, 1965) and glycol methacrylate sections were stained with "Periodic Acid" Schiff's reagent and toluidine blue (Feder and O'Brien, 1968).

FIGS 3-6.

Diagrams of transections of the stem of *Greyia* during abscission: 3, distal part of node with crescent-shaped leaf base; 4, basal part of node with diverging leaf traces; 5, median part of internode with break in separation layer starting at cortical ridge; 6, basal part of internode with pronounced break in separation layer: ab, axillary bud; ap, axial phloem group; cr, cortical ridge; cs, cortex of stem; e, epidermis; lb, leaf base; lt, leaf trace; ml, margin of leaf base; p, phellem; pd, phelloderm; px, primary xylem; s, separation layer; sc, sclerenchyma; vb, vascular bundle.





ANATOMICAL INVESTIGATION

A series of transverse sections of the one year old stem of *Greyia* reveals that the leaf has no sheath, but is connected to the stem at the node (figs. 3 & 4). The dilated, crescent-shaped leaf base partly encircles the node and the margins of the leaf base coincide with longitudinal ridges (figs. 4 and 5) on the internode. These ridges form the "margins" of the "leaf sheath" (fig. 1). The latter, therefore, is actually a broadened part of the cortex of the stem (figs. 4 & 5) which contains the leaf traces.

The leaf traces, which constitute the vascular supply of the leaf base (fig. 3), diverge at different levels of the internode from the vascular system of the stem to continue in the cortex. The first leaf trace branches off early, practically in the preceding node (fig. 6). In the median part of the internode three leaf traces

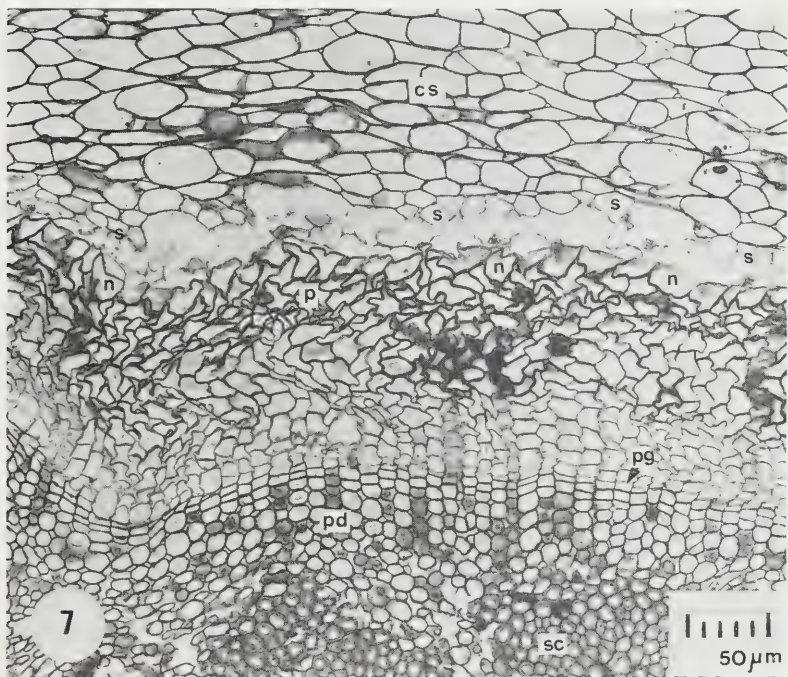


FIG. 7.

A part of a transection of the stem of *G. sutherlandii* illustrating the abscission zone; cs, cortex of stem; n, endodermis; p, phellem; pd, phelloderm; pg, phellogen; s, separation layer; sc, sclerenchyma group.

occur in the cortex (fig. 5). At the base of the node the remaining leaf traces are deflected into the leaf base (fig. 4).

During abscission the epidermis and the cortex abscise with the leaves. Abscission of these tissues commences at the base of the preceding internode (figs. 2 and 6) at the cortical ridges and the break in the tissues spreads around the circumference of the stem and acropetally towards the leaf bearing node (figs. 2, 5 and 6). In the vicinity of this node the epidermis and cortex are therefore still connected to the internal tissue of the stem although the abscission zone is already well developed (figs. 3 & 4).

According to Esau (1965), the abscission zone of the leaf consists of a separation layer, in which the actual break occurs, and a protective layer. In *Greyia* the periderm of the stem acts as the protective layer and comprises a multi-

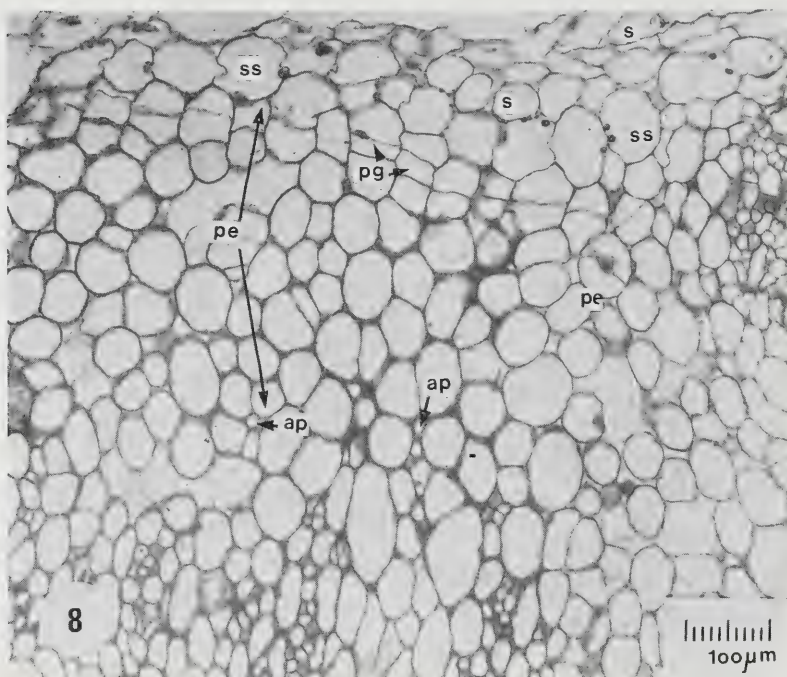


FIG. 8.

A part of a transection, approximately 300 μm below the promeristem, of the shoot of *G. radlkoferi* illustrating the starch sheath and origin of the phellogen: ap, axial phloem elements; pg, phellogen; pe, pericycle; s, separation layer; ss, starch sheath.

seriate layer of thin-walled, air-filled phellem cells, a phellogen layer and several layers of thin-walled phelloderm cells. The latter practically border the sclerenchyma caps lying on the outside of the axial phloem groups (fig. 7).

The phellogen, from which the protective layer arises, develops early in the ontogeny of the stem—the first traces of this meristem can already be seen in transections of the shoot apex, inside the starch sheath (fig. 8), which later becomes the endodermis (fig. 7). The dividing cells border the outermost axial phloem elements or may be separated from the latter by one to several layers of thin-walled cells, representing the pericycle.

The phellogen in the stem of *Greyia* therefore develops from the outermost layer of pericycle cells.

No specialized separation layer is formed in the leaf base of *Greyia* as often is the case in woody plants (Esau, 1965), but the inner cortical cells of the stem, through which the break occurs, are smaller, with thinner cell walls, than the adjoining cells of the cortex (fig. 7). The cell walls may therefore be mechanically weaker. This tissue can already be distinguished in the young stem on the outside of the starch sheath (fig. 8). Even in the stem apex the primordial leaves can easily be torn off in this region.

In the one year old shoot, therefore, the endodermis is that cell layer lying immediately outside the first layer of phellem cells and separating the latter from the inner cells of the separation layer. The endodermal cells contain no starch and the cell walls are thin and unlignified. The cells, however, are usually not destroyed during abscission, but remain attached to the periderm layer.

The reason for the unusual abscission phenomenon exhibited by *Greyia*, where the epidermis and cortex abscise with the leaves, therefore lies in the early development and the deep origin of a continuous abscission zone for all the leaves. The separation layer, as well as the phellogen of the protective layer, is already present in the extremely young shoot and extends throughout the nodes and internodes of the stem, in the vicinity of the endodermis. At the end of the growing season all the tissues outside the protective layer die off and abscise.

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REFERENCES

- ASHLEY, C. A. AND FEDER, N., 1966. Glycol methacrylate in histopathology. *Archs Path.* **81**: 391-397.
- ESAU, K., 1965. *Plant anatomy*. 2nd ed. London: Wiley and Sons.
- FEDER, N. AND O'BRIEN, T. P., 1968. Plant microtechnique: Some principles and new methods. *Am. J. Bot.* **55**: 123-142.
- GÜRR, E., 1965. *The rational use of dyes in biology and general staining methods*. London: Leonard Hill.
- HUTCHINSON, J., 1959. *The families of flowering plants*. Vol. 1. Dicotyledons. 2nd ed. Oxford: Clarendon Press.
- PHILLIPS, E. P., 1951. *The genera of South African flowering plants*. 2nd ed. Pretoria: Government Printer.
- SCHOLZ, H. 1964. Sapindales. In: H. Melchior, (ed.) *A. Engler's Syllabus der Pflanzenfamilien*. Vol. 2: 12th ed. Berlin: Borntraeger.